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Segregation from direction differences in dynamic random-dot stimuli

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Abstract

Previous research has shown that a field of random dots in which each dot alternates between a slow and a fast speed, can give rise to the percept of two superimposed sheets of moving dots when the alternations are out of phase or asynchronous with each other [Vis. Res. 35 (1995) 1691]. Under those conditions, observers can discriminate changes in the slow speed independent of changes in the fast speed. The present study investigated whether such motion-based segregation could result when dots alternated between two different directions. Three observers viewed a variety of displays containing two directions of motion, one upward and one oblique, with the task of discriminating small trial-to-trial changes in the direction of the upward component. The oblique direction component also changed direction from trial-to-trial. The field of dots either alternated synchronously (all dots moved in the same direction and switched to the other direction simultaneously) or asynchronously. Results showed that when the dots alternated synchronously between the directions, observers' direction discrimination performance was generally poor. However, when dots switched directions asynchronously, direction discrimination was only slightly elevated in comparison to that produced by a field of dots all moving in a single direction. Additional experiments demonstrated that this performance was not due to judging the global direction of the random-dot display. Thus the visual system had to segregate the stimulus into its component directions before integrating to arrive at the motion signal to be discriminated. It is concluded that for displays comprising elements that alternate between different directions, local direction signals can be used by the human visual system to effectively segregate a display so long as both direction signals are present simultaneously.

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1. Segregation from direction differences in dynamic random-dot stimuli

The percept of transparency arising in displays that contain two or more different motions has been of interest to vision researchers because of its relevance to understanding how the visual system encodes and interprets superimposed motion information. van Doorn and Koenderink identified conditions under which two independent dot patterns moving at different velocities would give rise to the percept of transparency. Their data show that rapidly alternating between the two moving patterns at a rate of 100 Hz led to a percept of transparency so long as the direction difference was 30° or greater (van Doorn & Koenderink, 1982a). More-

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over, if the display presented the two motion stimuli simultaneously but in alternate horizontal strips, a transparent percept was achieved if the height of the strips was small (i.e., 2' for speeds of $0.26^{\circ} \text{ s}^{-1}$), though this value scaled with the speed of the stimulus (van Doorn & Koenderink, 1982b). These early data suggest that transparency relies on the visual system encoding two (or more) distinct motion signals (that maximally stimulate separate populations of motion detectors) that are identified and maintained as separate signals. Similarly, Bravo and Watamaniuk (1995) showed that if two spatially overlapping sets of dots moved at speeds that differed by about a factor of 2, segregation occurred and the percept was one of transparency. Under these conditions, observers could discriminate small changes in the speed of one component independent of the other component. More surprising, if every dot in the stimulus alternated between the two component speeds segregation still occurred. However, this alternation had to be asynchronous such that only a portion of the dots

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changed speed each frame so that both component speeds were simultaneously present in the display—if all dots changed speed synchronously or if the stimulus contained only a single dot alternating between the two speeds, judgement of one of the component speeds was impossible. Bravo and Watamaniuk concluded that the segregation was based on coarse local speed signals but that the more precise speed signal used for discrimination was the result of integrating similar local speeds over space and time.

The present study sought to determine if segregation and transparency could result from a random-dot stimulus comprised of dots that alternated between two directions of motion. Thus, similar to Bravo and Watamaniuk (1995) and unlike van Doorn and Koenderink (1982a), both direction signals would be carried by the same population of dots. In past studies, presenting a random-dot cinematogram (RDC) in which each dot randomly selects a new direction of motion each frame from a continuous range of directions has resulted in the percept of the field of dots moving in a single common direction. This single direction percept relies on the spatial and temporal integration of local direction information and has been referred to as global flow or coherent motion (e.g., Smith, Snowden, & Milne, 1994; Watamaniuk & Sekuler, 1992; Watamaniuk, Sekuler, & Williams, 1989; Williams & Sekuler, 1984). The distribution from which the dots select their direction each frame does not even have to be continuous or even nearly so in order for global flow to be perceived; observers were unable to discriminate the global flow produced by a stimulus whose directions were being chosen from a large distribution ($180^{\circ}-270^{\circ}$) sampled either every 1° or every 25°–30° (Williams, Tweten, & Sekuler, 1991). Thus global flow results from an integration of the different direction signals but for transparency, the different direction signals must remain segregated.

Consistent with van Doorn and Koenderink (1982a), if a random-dot display is comprised of sets of dots moving in two directions separated by about 20°-30°, the percept is one of transparency. However, the direction of each of the two component directions is misperceived such that the two directions shift away from each other, a phenomenon called motion repulsion (Hiris & Blake, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Rauber & Treue, 1999). These studies found that as the difference between the two directions increases, the repulsion effect also increases until the directional difference between the two components reaches about 20°-30°. As the direction difference between the two components increases further, the repulsion effect decreases. Taken together, the data suggest that stimuli composed of discrete directions can lead to either an integrated global percept (Williams et al., 1991) or a percept of transparency (van Doorn & Koenderink, 1982a). In fact, Zohary, Scase, and Braddick (1996)

have suggested that under certain stimulus configurations, observers can voluntarily choose which percept, either the global flow or component directions, to make judgements about. Specifically, if stimuli contain a distribution of directions but have a well defined modal direction, observers can make judgements about either the modal or mean direction.

The above experiments suggest that two superimposed patterns of elements moving in different directions will result in the percept of transparency if the difference between the component directions is large enough (e.g., van Doorn & Koenderink, 1982a). However, if the elements randomly choose a new direction each frame from even a sparsely sampled distribution of directions, the percept is one of global flow (e.g., Williams & Sekuler, 1984; Williams et al., 1991). In the present study, we tested whether displays in which individual elements alternated between two directions of motion could produce a transparent percept. Specifically, we tested whether the same kind of rules for integration/segregation observed in displays in which elements alternated between two different speeds (Bravo & Watamaniuk, 1995) would also apply to displays in which elements alternated between two different directions.

2. Methods

2.1. Observers

Data for all experiments were collected from two of the authors (JF and ES) with additional data for some of the experiments from the third author (SW). All observers had normal or corrected to normal visual acuity. Observers JF and ES had no previous experience in psychophysical tasks and were naive to the purposes of the experiments.

2.2. Stimuli

The stimuli were RDCs displayed on a Tektronix oscilloscope (P4 phosphor) at a rate of 60 Hz. On the first frame of the cinematogram the positions of the dots were chosen randomly; on successive frames all dots were displaced a predetermined direction with equal step sizes producing a speed of 16° s⁻¹. When a dot reached the edge of the display, it wrapped around to the opposite side of the display. For most conditions, two directions of motion were presented in the stimulus, an upward direction and an oblique direction counterclockwise of upward. In the experiments, we will refer to four different types of displays: (1) single direction, (2) constant direction, (3) synchronous alternation, and (4) asynchronous alternation. We will describe each of these stimuli in detail here and refer to them by name

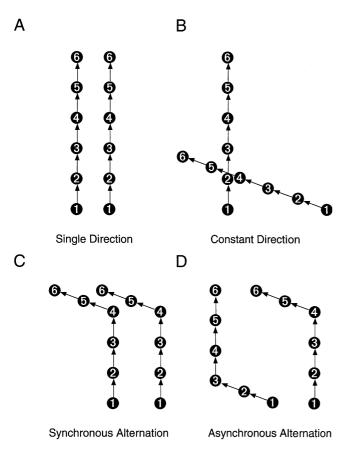


Fig. 1. A schematic representation of the four stimulus conditions. Each panel depicts two dots' motions over six presentation frames. The numbers in each dot represent the frame in which the dot appears at that position. In the single direction condition (panel A), all dots move in the same direction for the duration of the display. In the constant direction condition (panel B), one-half of the dots move in an upward direction while the other half move in an oblique direction for the duration of the display. In the synchronous alternation condition (panel C), all dots start by moving in one direction (upward in this depiction) and then alternate to the other direction (oblique) at consistent intervals throughout the stimulus presentation. In the asynchronous alternation condition (panel D), individual dots moved in the same way as in the synchronous condition but the alternations in direction were not simultaneous across dots. In every frame, a set proportion of dots changed direction from upward to oblique and vice versa.

throughout the rest of the paper. Fig. 1 shows schematic representations of each of the four stimulus types.

(1) Single direction (Fig. 1A): In this stimulus, 128 dots were displayed and all moved in the same direction from frame-to-frame. This condition provided the baseline to which other discrimination performances will be compared.

(2) Constant direction (Fig. 1B): In this stimulus, the dots were divided randomly into two sets, each containing 128 dots. One set moved in an upward direction (centered around 90°) and the other moved in an oblique direction counterclockwise of upward (centered around 160°).

(3) Synchronous alternation (Fig. 1C): In this stimulus, 256 dots moved in one direction (either upward or oblique) for some temporal interval, then all dots switched to the other direction for the next temporal interval, then all dots switched back to the first direction and so on. The duration spent at each direction varied depending upon the experimental condition. Thus, although both directions of motion were present in every display, only a single direction of motion was presented at any given moment.

(4) Asynchronous alternation (Fig. 1D): In this stimulus, the behavior of the individual dots was identical to that of the dots in the synchronous alternation stimulus; dots alternated between moving in the upward and oblique directions. The difference was that the dots did not change direction at the same time, the direction changes of the dots were asynchronous or out of phase with each other. Thus, both directions of motion were always present in the display in a dynamic, spatially distributed random pattern.

For all conditions, stimulus duration was held constant at 533 ms (32 frames) and observers viewed the display binocularly from a distance of 57 cm. A 10° diameter circular mask covered the $10 \times 10^{\circ}$ screen to remove potential orientation cues provided by the edges of the screen. Dots subtended 4.2' and had a spaceaveraged luminance of 53.4 cd/m² while the veiling luminance of the screen was 26.0 cd/m² (space-averaged luminance was measured using a matrix of dots with a center-to-center spacing of 4.8' and a frame rate of 60 Hz).

2.3. Procedure

Direction discrimination thresholds were measured using the method of single stimuli; in each trial, a single stimulus was presented and the observer had to judge whether its direction was clockwise or counterclockwise of the mean direction. Observers fixated on a central stationary spot during the stimulus presentation and responded at the end of a trial by pressing one of two buttons, corresponding to clockwise and counterclockwise, to indicate their judgement. Feedback indicated an incorrect response.

For most experiments, the stimuli contained two directions of motion, upward and oblique, and observers made judgements about the upward direction. Under these conditions, there were five possible upward directions centered around 90° and five possible oblique directions centered around 160° (counterclockwise from upward). Within a single experimental block, the observer was presented every possible pairing of upward and oblique directions (25 total stimuli) 10 times in a random order. Although observers were only required to judge the upward direction, varying the oblique direction made the relative difference between the two component directions and the average direction of the stimulus unreliable cues on which to make a judgement. The spacing of the five oblique directions within a block was also manipulated to be either 0° (constant), 1° , 2° , or 10° . This manipulation did not affect discrimination performance but served to further reduce the informativeness of the oblique direction. In order for the observers to determine the mean upward direction against which to make their judgements, each experimental session started with 10 practise trials. The two main observers performed about 4000 practise trials on this task before data collection began.

For each 250 trial block, the number of 'clockwise' responses for each of the upward directions was used to generate a psychometric function. The data were fit with a cumulative normal distribution using probit analysis (Finney, 1964). Direction discrimination thresholds were defined as half the directional difference necessary to change performance levels from 25% to 75%. Between 2 and 5 thresholds per condition were obtained from each subject. Standard errors of the mean were computed for each subject based on the thresholds obtained in each condition.

3. Experiment 1: Direction discrimination for transparent stimuli

In this first experiment, we measured direction discrimination for the constant direction condition in which the display comprised two independent sets of dots, one moving upward and the other moving obliquely. This display was perceived consistently as two transparent sheets of dots sliding over each other. Even though the directions appeared clearly segregated, it is of interest to know if having two directions in the same visual space alters the discrimination of one component direction. For comparison, direction discrimination for the single direction condition was used as baseline data.

3.1. Results and discussion

Fig. 2 shows data for three observers for the single direction and constant direction conditions. Each observer completed two thresholds for each condition and each observer's data were analyzed separately. Individual *t*-tests showed that for all three observers, there was no significant difference between direction discrimination performance under the single direction and constant direction conditions (JF: t(2) = 1.47; ES: t(2) = 3.59; SW: t(2) = 2.67, p > 0.05). Though not significant, thresholds were slightly higher in the constant direction than in the single direction condition. This suggests that the presence of a superimposed moving pattern differing by about 70° has only a slight

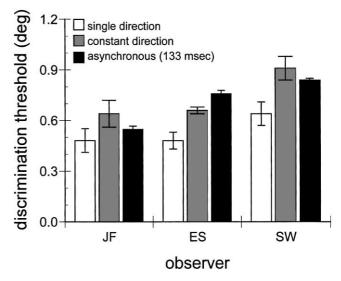


Fig. 2. Direction discrimination thresholds (°) for the three observers for the single direction, constant direction, and asynchronous alternation conditions. In the asynchronous alternation condition, dots changed their direction of motion every 8 frames (133 ms). Error bars represent ± 1 standard error of the mean.

influence on the precision of the direction judgement and on average increased thresholds by 0.2° . There are three possible reasons for this increase in thresholds. First, it may be that the two directions of motion are not completely segregated by the visual system (i.e., the encoding of directions is not independent) but the statistical test had too little power to reveal the significant effect. Second, the small increase in thresholds may be due to the effects of motion repulsion. When two superimposed sets of dots move in directions that differ by up to 90°, the directions of the components are consistently perceived as shifted away from the other component (i.e. Marshak & Sekuler, 1979). For a difference in direction near 70° , like that used in the present study, this shift in perceived direction can range from about 2° to 5° (Hiris & Blake, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Rauber & Treue, 1999). Since the stimulus' oblique direction varied from trial-to-trial, one cannot easily estimate the overall size of the repulsion effect in the present data. Finally, Braddick (1997) found that in transparent displays comprised of two different directions, performance for judging whether the direction difference was greater or less than 90° was larger than that predicted by the directional error associated with each direction component. Braddick proposed that this elevation may be the result of some interference or interaction in the direction representations (other than motion repulsion) that occurs when computing two directions at the same time. The present stimuli would also be subject to this type of interference and thus may be responsible, in part, for the slight increase in discrimination thresholds. This issue will be readdressed in Section 7.

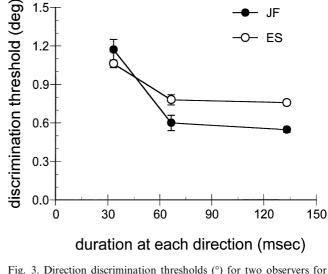
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4. Experiment 2: Segregation when dots alternate directions

The previous data showed that if a display is composed of two independent sets or patterns of dots, people are able to separate the motion signals arising from each and judge one direction essentially independent of the other. This experiment was designed to determine if the visual system can separate the direction signals of objects that alternate between two different directions or if the direction information is averaged over time. For this test, we compared performance for a stimulus in which the component dots alternated asynchronously between two directions every 133 ms (asynchronous alternation condition) to that for the constant direction condition. Thus the stimuli in each condition contained the same direction information distributed differently over time among the component dots. We also tested whether that duration that a dot traveled in a particular direction influenced direction discrimination. For this purpose, we had observers judge a component direction in asynchronously alternating displays in which the alternation rate was varied from 30 Hz (direction alternations every 33 ms) to 7.5 Hz (direction alternations every 133 ms). ¹ Only two observers completed the entire duration series.

4.1. Results and discussion

The data for the 133 ms asynchronous alternation are plotted in Fig. 2 for easy comparison to the constant direction data. Observers JF and ES completed nine thresholds for the asynchronous condition while observer SW completed two thresholds. Each observer's data were analyzed separately. Notice that while two observers had a lower threshold for the asynchronous than the constant direction condition, the other observer showed the opposite pattern. For all observers, however, the difference between conditions was small. Individual t-tests showed that performance was not significantly different between the asynchronous alternation and constant direction condition (JF: t(9) = 1.62; ES: t(9) = 1.78; SW: t(2) = 0.976, p > 0.05). Thus in the asynchronous condition, observers were able to judge the direction of one component direction even though no object moved continuously in that direction. The observers' perceptual experience of the alternating displays were consistent with their discrimination ability. The alternating displays were perceived as containing two distinct sheets of dots moving in different directions, although the dots composing each pattern were not



the asynchronous alternation condition for three different alternation rates: direction alternations every 33, 67, and 133 ms. The error bars represent ±1 standard error of the mean. Notice that thresholds decrease when the duration at each direction increases from 33 to 67 ms but do not decrease with further increases in duration. Note that as the duration at each direction increases from 33 to 133 ms, alternation rate decreases from 30 to 7.5 Hz.

constant. Data for the effect of duration is presented in Fig. 3 for two observers, with the data point for the 133 ms condition being the same as that plotted in Fig. 2. Both observers completed nine thresholds for the 33 and 133 ms conditions but only four (JF) or three (ES) thresholds for the 67 ms condition. Notice that for both observers, thresholds are higher for the 33 ms alternations but similar for the 67 and 133 ms alternations. One-way ANOVAs conducted on each observer's data showed that there was a significant difference among the three alternation rates (JF: F(2, 19) = 32.17; ES: F(2, 18) = 29.3, p < 0.05). At an alpha level of 0.05, a post hoc Scheffe's S test showed that while the performance for the 33 ms alternation condition was significantly poorer than both the 67 and 133 ms conditions, there was no significant difference between the 67 and 133 ms conditions.

5. Experiment 3: Performance with synchronous direction changes

The previous experiment showed that direction discrimination performance can be as good for an RDC in which each dot changes its direction of motion asynchronously every 67-133 ms as an RDC that contains two sets of dots that maintain their direction over the entire stimulus presentation. There are two possible hypotheses that can account for the data: (1) the visual system is segregating the alternating stimuli as effectively as those that contained two overlapping patterns of

JF

¹ Here we use the term 'alternation frequency' to denote the frequency at which a dot changes its motion from one direction to the other, rather than the frequency at which a dot completes whole cycles, changing from one direction to the other and back again.

dots, or (2) observers may have been making their decisions based upon the motion of one or a small number of dots over a short time period. The second hypothesis suggests that in the alternating conditions, if the visual system could isolate the direction of motion of a dot or dots for 67-133 ms, the direction signal may be good enough to perform the discrimination task well. To test between these two hypotheses, observers performed the direction discrimination task under two stimulus configurations. In one condition, observers were shown a stimulus containing a single dot that moved for a duration of 67 ms. The dot appeared near the center of the display, with a random horizontal and vertical offset, and observers judged its direction as in the previous experiments. In the second condition, observers were shown a stimulus containing two directions of motion but all dots moved in one direction for a either 67 or 133 ms and then changed synchronously to the other direction of motion for the same duration and then switched back to the first direction etcetera (see Section 2 for a detailed description). The logic here is that if observers were able to make their direction judgements by isolating the direction of one or a small number of dots for a few frames, then performance should be similar in any stimulus that provides such direction information. Thus, discrimination in the single-dot condition and the 67 ms synchronous condition should be similar. In addition, since the synchronous condition contains the same direction information as the asynchronous condition from the previous experiment with only the timing of the changes between dots being different, we also expect that performance in the synchronous condition to be similar to that for the asynchronous conditions from Experiment 2.

5.1. Results and discussion

The results for the two observers appear in Fig. 4. Data from the previous experiment for the two asynchronous conditions are plotted for reference. For the synchronous conditions, observer JF completed four thresholds for the 67 ms condition and nine for the 133 condition while observer ES completed three ms thresholds for the 67 ms condition and nine for the 133 ms condition. Both observers completed only one threshold for the single-dot condition and its error bars were computed from the probit fits. As can be seen in the figure, performance in the asynchronous and singledot conditions is better than performance in the synchronous conditions. ANOVAs on the individual's data confirmed a significant effect of condition (JF: F(4, 22) = 76.58; ES: F(4, 20) = 27.4, p < 0.05). With alpha set at 0.05, a post hoc Scheffe's S test for each observer revealed that while there was no significant difference among the asynchronous and single-dot conditions, there was a significant difference in performance

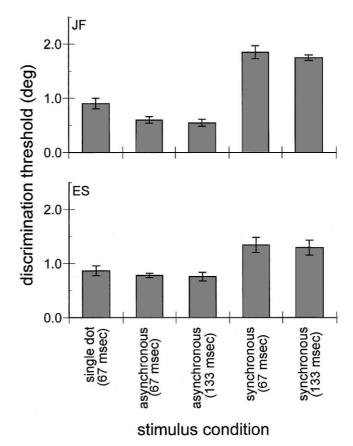


Fig. 4. Direction discrimination thresholds (°) for the two observers for the single dot (67 ms), two asynchronous (67 and 133 ms) and two synchronous (67 and 133 ms) conditions. Error bars represent ± 1 standard error of the mean except for the single-dot condition for which standard errors were computed from the probit fits. The asynchronous data are replotted from Fig. 3. Notice that the single dot and asynchronous thresholds are similar while those for the synchronous conditions are significantly higher.

between these conditions and the synchronous conditions. No significant difference was found between the two synchronous conditions. A third observer, SW, produced results similar to these but since only one threshold per condition was completed, no statistical analysis could be performed. These results suggest that it is unlikely that observers were making their judgements of direction based upon the movement of a single dot in the multi-dot displays since both the asynchronous and synchronous displays should have resulted in thresholds similar to the single-dot display.

6. Experiment 4: Are observers judging global motion?

The previous experiment tested whether observers were using the motion information during brief intervals of a dot's constant motion to base their direction judgement. The results suggested that the observers were not using such a strategy. However, another alternative is that observers were basing their judgements on a global motion signal by integrating the direction signals over the entire display (e.g., Smith et al., 1994; Watamaniuk et al., 1989; Williams & Sekuler, 1984) even when the directions in the display were perceived as segregated. This hypothesis can be logically dismissed by looking at the data already presented. If global motion were the basis of the direction judgements then the constant direction, asynchronous and synchronous conditions should have resulted in similar performance because they contained identical global motion information. Fig. 2 showed that while the constant direction and asynchronous (67 and 133 ms) conditions produced similar performance, Fig. 4 clearly shows that the synchronous conditions produced poorer performance. However, to directly test whether global motion could be the basis of the discrimination thresholds measured in the previous experiments, the asynchronous and synchronous conditions were repeated but giving the observers explicit instructions to judge the global direction of motion. As an additional comparison, global direction discrimination thresholds were also measured around a mean direction of 125° for a typical global flow stimulus in which the dots were randomly assigned a direction of motion each frame from a uniform distribution of directions spanning 70° (e.g., Watamaniuk et al., 1989). This mean direction and range are similar to those of the asynchronous and synchronous stimuli.

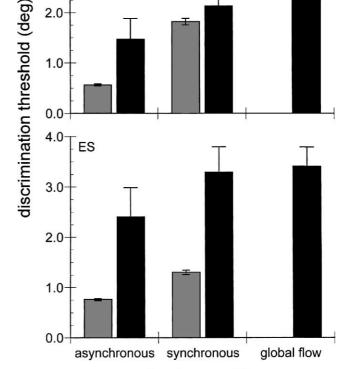
6.1. Results and discussion

Results for global direction discrimination for the asynchronous, synchronous, and global flow conditions appear in Fig. 5 along with thresholds for judging the upward component for the asynchronous and synchronous conditions (from Fig. 4). Note that because of their similarity, the respective 67 and 133 ms asynchronous and synchronous component thresholds have been combined for this analysis. Observer JF completed nine global direction thresholds each for asynchronous and synchronous conditions while observer ES completed 10 global direction thresholds for the asynchronous and 12 global direction thresholds for the synchronous conditions. Both observers completed five thresholds for the global flow stimulus. To determine if the component thresholds differed from the global direction and global flow thresholds, t-tests were performed on each individual's data. ANOVAs were not computed since there are no predictions nor expectations regarding interactions. The *t*-tests showed that the global direction thresholds for the asynchronous condition were significantly higher than their respective component motion thresholds for (JF: t(20) = 2.67; ES: t(20) = 3.10, p < 0.05). However, for the synchronous condition, the global direction threshold was significantly higher than the component threshold for observer ES (t(22) = 3.96,

Fig. 5. Direction discrimination thresholds for two observers for asynchronous and synchronous conditions, as well as a global flow stimulus comprised of a uniform distribution of directions sampled every 1° spanning a range of 70° (mean direction of 125°). Thresholds obtained when observers were asked to judge the upward component direction are represented by the grey bars and those obtained when observers were asked to judge the global stimulus direction appear as solid bars. Observers only judged the global direction for the global flow stimulus. Error bars represent ± 1 standard error of the mean. Notice that component direction thresholds were always lower than the global direction thresholds.

stimulus condition

p < 0.05) but not for observer JF (t(20) = 1.783, p = 0.09). These data reinforce the idea that at least for the asynchronous condition, the global direction of motion was not the cue used for the discrimination of the upward component direction. Additionally, the discrimination thresholds for the global flow stimulus were also significantly greater than the asynchronous component thresholds (JF: t(16) = 14.0; ES: t(15) = 11.14, p < 0.05) and the synchronous component thresholds (JF: t(15) = 8.57, p < 0.05). Compared to the asynchronous global direction thresholds, the global flow stimulus produced significantly higher thresholds for observer JF (t(12) = 2.25, p < 0.05) but not for observer ES (t(13) = 1.15, p > 0.05). There were no significant differences between



4.0

3.0

JF

component

global

the synchronous global direction and the global flow thresholds. Although these results are not conclusive, it seems that observers may be better able to determine the global direction for a stimulus that contains only two directions separated by 70° rather than a distribution spanning the same range.

7. General discussion

The present study was conducted to investigate the mechanism by which the visual system segregates superimposed moving stimuli that differ in direction. To this end, direction discrimination thresholds were measured for a variety of stimuli containing two directions of motion. The rationale was that if the visual system can segregate the two directional signals then observers should be able to discriminate one component direction essentially independent of the other. Thus the discrimination thresholds were used as an indicator of segregation. Several important points can be made from the results. First, direction discrimination thresholds for displays containing two superimposed sets of dots moving in different directions were only slightly higher than thresholds for a single set of uniformly moving dots (see Fig. 2, constant vs single direction). This small elevation in direction discrimination could have been due to incomplete segregation of the two motion signals, motion repulsion effects (i.e. Marshak & Sekuler, 1979), or other interference between the two motion signals (Braddick, 1997). Direction discrimination thresholds were considerably higher under conditions which seem to foster integration rather than segregation, such as the synchronous and global direction conditions, making it unlikely that incomplete segregation was the cause of the slight elevation in the constant direction condition. Thus it seems that motion repulsion and interference contribute to the elevated thresholds, however, our data cannot be used to determine the magnitude of these effects independently. Even with the slight elevation, thresholds were all less than 1° which is equal to or better than previously published direction thresholds (e.g., Watamaniuk, 1993; Watamaniuk & Sekuler, 1992; Watamaniuk et al., 1989; Westheimer & Wehrhahn, 1994). This represents excellent discrimination performance in a situation that contains potentially catastrophic directional noise if the directional signals are not processed separately. Second, when two directions of motion were present, performance was unchanged whether there were two independent sets of dots, each moving in a constant direction, or if dots alternated asynchronously between the two directions (see Fig. 2). However, optimal performance was not achieved unless the duration spent at each direction was longer than 33 ms (see Fig. 3). This is consistent with the study by Bravo and Watamaniuk (1995) in which speed discrimination improved, using analogous asynchronouslyalternating two-speed displays, as the duration spent at each speed in the alternating display increased from 33 to 133 ms.

Interestingly, performance with asynchronously alternating stimuli was not significantly better than that for a single dot that moved in a constant direction for a duration equivalent to one 67 ms alternation (see Fig. 4). But the data suggest that performance was not based upon the direction signal generated by one dot as it moved in a constant direction over some small time interval (67–134 ms). If this were true, then performance in the asynchronous and synchronous conditions should be equivalent, as both provide equivalent local direction information. However, performance was significantly poorer when the alternations were synchronous. Thus, the visual system seems to use the different but simultaneously present local motion signals to segregate the display and then it integrates those local signals over space and time. The data also show that component direction judgements were based upon the target component direction rather than the global direction of the stimulus (see Fig. 5). This reinforces the interpretation that in displays that produced segregated percepts and good component discrimination, processing of one component direction was little influenced by the processing of the other component direction. However, it also appears that observers can voluntarily modulate which scale of motion they judge. Specifically, observers were able to make judgements of global motion for the asynchronous and synchronous displays that were similar to thresholds obtained with a typical global flow stimulus (e.g., Watamaniuk et al., 1989). This finding is consistent with Zohary et al.'s (1996) report that for their stimuli, observers could judge either the global or component direction on request. This suggests that how motion signals are processed may be under some observer control or that observers can choose which level of processing they access to make a judgement as suggested by Watamaniuk and McKee (1998).

Direction discrimination has been previously measured for transparent random-dot stimuli by Smith, Curran, and Braddick (1999). Their stimuli comprised two sets of dots that chose their direction of motion from two independent direction distributions spanning variable ranges. They found that when the two component directions in the transparent stimuli differed by 90° and had distribution widths of 0° (each set of dots moved in only a single direction), direction discrimination was much poorer than that for control stimuli that contained only a single direction of motion. The present results seem to be at odds with these findings since we found only a slight increase in thresholds in the transparent asynchronous condition. One clear difference between the Smith et al. study and ours is that in their stimuli the dots had lifetimes of only two frames or one displacement. Short dot lifetimes likely do not stimulate motion detectors optimally because the motion signal usually spans less than the size of a motion detector receptive field (up to 1°) nor does it last as long as a detector's integration time (about 100 ms). Limitedlifetime dots also produce additional visual noise because all motion detectors, regardless of their direction or speed tuning, will respond to the transient flash produced by the random relocation of a dot if it falls within their receptive field. Thus the two-frame dot lifetime used by Smith et al. likely resulted in noisier local direction estimates, making segregation of the motion signals more difficult and causing direction thresholds to be larger. Consistent with this notion of poorer motion signals and increased visual noise, a separation of 45° between the directions of the two sets of dots (with a 0° distribution width) did not lead to a percept of transparency. This is not consistent with Williams et al. (1991) nor van Doorn and Koenderink (1982a) who found that a difference of only 30° resulted in transparency when the stimuli used dot whose lifetimes were equal to the presentation duration. This suggests that caution should be used when comparing performances across studies that have employed different random-dot algorithms. The limitations of limitedlifetime dots also seems to be in line with Smith et al.'s (1999) conclusion that "transparency involves a highquality, quantitative representation of component motions", (p. 1129).

The present results, along with those of Bravo and Watamaniuk (1995) reveal an interesting characteristic of the visual system. If elements in a display alternate between different motions but there is only one direction or speed of motion present at any moment, the percept appears to be that of a single object undergoing a dynamic change in motion-motion integration occurs and judgements of component motions are poor. If there are two directions or speeds of motion present simultaneously and each lasts long enough to produce a good local motion estimate (e.g., at least 30-50 ms), the percept is that of two transparent surfaces. In other words, the visual system uses the simultaneously present local motion signals to segregate the motions in the display, suggesting that the visual system has processed the different motions as arising from different objects. After this segregation, an integrative process follows but only similar motion signals are integrated over space and time to extract a more precise motion measure and then each motion can be judged virtually independent of the other. Results that are seemingly contradictory to this idea have been reported by van Doorn and Koenderink (1982a). These researchers found that two directions of motion need not be simultaneously present to lead to a percept of transparency. In their study, alternation of two dot patterns moving in opposite directions could lead to the percept of transparency if the alternation rate was high

enough. For speeds comparable to those used in the present study, transparency was perceived when the alternation rate was about 100 Hz, such that the duration of each motion was 10 ms. The present experiment did not test alternation rates that high so no direct comparison is possible. However, it may be that at high alternation rates, the motion information is essentially simultaneously present in the visual system because of the approximately 100 ms integration time of the motion detectors (e.g., Reid, Soodak, & Shapley, 1991).

In conclusion, when a random-dot display contains overlapping sets of dots moving in two different directions, segregation based upon direction of motion can occur even when the dots alternate between the two component motions so long as they do so asynchronously. This asynchronous alternation means that the elements carrying each direction signal change dynamically throughout the course of the display. Thus segregation and transparency can occur at the expense of losing surface element integrity. This may suggest that motion consistency is weighted more heavily in scene segregation than textural consistency.

References

- Braddick, O. J. (1997). Local and global representations of velocity: transparency, opponency, and global direction perception. *Perception*, 26, 995–1010.
- Bravo, M. J., & Watamaniuk, S. N. J. (1995). Evidence for two speed signals: A coarse local signal for segregation and a precise global signal for discrimination. *Vision Research*, 35, 1691–1697.
- Finney, D. J. (1964). *Probit analysis*. Cambridge: Cambridge University Press.
- Hiris, E., & Blake, R. (1996). Direction repulsion in motion transparency. Visual Neuroscience, 13, 187–197.
- Marshak, W., & Sekuler, R. (1979). Mutual repulsion between moving visual targets. *Science*, 205, 1399–1401.
- Mather, G., & Moulden, B. (1980). A simultaneous shift in apparent direction: Further evidence for a distribution-shift model of direction coding. *Quarterly Journal of Experimental Psychology*, 32, 325–333.
- Rauber, H.-J., & Treue, S. (1999). Revisiting motion repulsion: evidence for a general phenomenon. *Vision Research*, 39, 3187– 3196.
- Reid, R. C., Soodak, R. E., & Shapley, R. M. (1991). Directional selectivity and spatiotemporal structure of receptive fields of simple cells in cat striate cortex. *Journal of Neurophysiology*, 66, 505–529.
- Smith, A. T., Curran, W., & Braddick, O. J. (1999). What motion distributions yield global transparency and spatial segmentation. *Vision Research*, 39, 1121–1132.
- Smith, A. T., Snowden, R. J., & Milne, A. B. (1994). Is global motion really based on spatial integration of local motion signals? *Vision Research*, 34, 2425–2430.
- van Doorn, A. J., & Koenderink, J. J. (1982a). Temporal properties of the visual detectability of moving spatial white noise. *Experimental Brain Research*, 45, 179–188.
- van Doorn, A. J., & Koenderink, J. J. (1982b). Spatial properties of the visual detectability of moving spatial white noise. *Experimental Brain Research*, 45, 189–195.
- Watamaniuk, S. N. J. (1993). An ideal observer for discrimination of the global direction of dynamic random dot stimuli. *Journal of the Optical Society of America A*, 10, 16–28.

- Watamaniuk, S. N. J., & McKee, S. P. (1998). Simultaneous encoding of direction at a local and global scale. *Perception and Psychophysics*, 60, 191–200.
- Watamaniuk, S. N. J., & Sekuler, R. (1992). Temporal and spatial integration in dynamic random-dot stimuli. *Vision Research*, 32, 2341–2347.
- Watamaniuk, S. N. J., Sekuler, R., & Williams, D. W. (1989). Direction perception in complex dynamic displays: The integration of direction information. *Vision Research*, 29, 47–59.
- Westheimer, G., & Wehrhahn, C. (1994). Direction discrimination of motion in human vision. *Journal of Neurophysiology*, 71, 33–37.
- Williams, D. W., & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, 24, 55–62.
- Williams, D., Tweten, S., & Sekuler, R. (1991). Using metamers to explore motion perception. *Vision Research*, *31*, 275–286.
- Zohary, E., Scase, M. O., & Braddick, O. J. (1996). Integration across directions in dynamic random dot displays: Vector summation or winner take all? *Vision Research*, 36, 2321–2331.